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Research Reports

AN AUTORADIOGRAPHIC STUDY OF THE PROJECTIONS FROM THE LATERAL GENICULATE BODY OF THE RAT

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SUMMARY

The projections from the lateral geniculate body of the rat were followed using the technique of autoradiography after injections of [^3H]proline into the dorsal and/or ventral nuclei of this diencephalic structure. Autoradiographs were prepared from either frozen or paraffin coronal sections through the rat brain. The dorsal nucleus of the lateral geniculate projected via the optic radiation to area 17 of the cerebral cortex. There was also a slight extension of label into the zones of transition between areas 17, 18 and 18a. The distribution of silver grains in the various layers of the cerebral cortex was analyzed quantitatively and showed a major peak of labeling in layer IV with minor peaks in outer layer I and the upper half and lowest part of layer VI. The significance of these peaks is discussed in respect to the distribution of geniculocortical terminals in other mammalian species.

The ventral nucleus of the lateral geniculate body had 5 major projections to brain stem structures both ipsilateral and contralateral to the injected nucleus. There were two dorsomedial projections: (1) a projection to the superior colliculus which terminated mainly in the medial third of the stratum opticum, and (2) a large projection via the superior thalamic radiation which terminated in the ipsilateral pretectal area; a continuation of this projection passed through the posterior commissure to attain the contralateral pretectal area. The three ventromedial projections involved: (1) a geniculopontine tract which coursed through the basis pedunculi and the lateral lemniscus to terminate in the dorsomedial and dorsolateral parts of the pons after giving terminals to the lateral terminal nucleus of the accessory optic tract, (2) a projection via Meynert's commissure to the suprachiasmatic nuclei of both sides of the brain stem as well as to the contralateral ventral lateral geniculate nucleus and lateral terminal nucleus of the accessory optic tract, and (3) a medial projection to the ipsilateral zona incerta. The results obtained in these experiments

are contrasted with other data on the rat's central visual connections to illustrate the importance of these connections in many subcortical visual functions.

INTRODUCTION

Due to its location in the brain stem, study of the projections of the lateral geniculate body in the rat has proved to be a difficult task. Most efforts to produce lesions in this nucleus run into the danger of interrupting either axons in the optic tract or in the brachium of the superior colliculus. The use of the autoradiographic tracing method obviates the problem of causing degeneration of axons of passage^{7,21} and at the light microscope level¹⁶ autoradiographic tracing has been shown to be at least as sensitive as the Fink-Heimer technique in determining axonal projections. In a recent study on the retinogeniculate pathways in the cat and the fox¹⁷, autoradiography has been more precise than fiber degeneration studies since it displayed an extra layer in the geniculate which received terminals from the retina.

The lateral geniculate body in the rat is divided into dorsal (dLGN) and ventral (vLGN) nuclei by a bundle of horizontally oriented fibers (Fig. 1A). In a study of the lateral geniculate body of the rat, Brauer and Schober³ have demonstrated two types of neurons in the dLGN and two in the vLGN. The type I cell in the dLGN was described as a neuron that functioned as a geniculocortical relay cell. The type II cell was smaller and was considered to be an interneuron. These cells are distributed equally throughout the dLGN. The type III and IV cells found in the vLGN were similar to the type I and II cells. However, they had a preferential location. The type III cells resided in the lateral vLGN whereas the type IV cells were in the medial zone of that structure.

The projection of the dLGN to the visual area in the rat cerebral cortex was shown by the experiments of Lashley²². After destroying parts of the cerebral cortex and observing retrograde degeneration in thionin-stained sections, he concluded that the field of termination of the dLGN was restricted to the area striata. Following such removals of cortex, the neurons of the vLGN were not observed to undergo any degeneration and it was thus concluded that this subdivision of the lateral geniculate body did not contribute to the optic radiation. Due to the nature of the methods used by Lashley²², it was not possible to comment on the distribution of thalamocortical afferents to the different layers of the visual cortex. Similar results had been obtained by both Clark⁶ and Waller⁴⁰.

Krieg²⁰ employed the method of lesioning a thalamic nucleus followed by the staining of degenerating myelin sheaths with the Marchi method to study the thalamocortical projections in the rat. However, he did not report data for the dLGN projections to the striate cortex because no lesions included this thalamic nucleus. In fact, there have been no reported studies on the distribution of dLGN axon terminals in the visual cortex of the rat. There have been many studies on the pattern of degenerating terminals in the layers of visual cortex in other mammals and Polley³¹ found terminals in layers IV and I in the cat and layers IV, III and I in the rhesus monkey. Most authors^{1,24,35} have described the greatest concentration of degener-

ating terminals to be in layer IV, although they have also referred to fine pericellular degeneration in layers VI, V and I. Further proof for geniculocortical afferents ending in layer VI has recently been demonstrated in the cat using the autoradiographic technique for tracing pathways³⁴.

The vLGN of the rat was described by Gurdjian¹² as having projections to the zona incerta and to contralateral structures via Meynert's commissure, while Tsang³⁹ theorized that there is a vLGN projection to the contralateral vLGN and to the pretectal area via Meynert's commissure.

While this work was being prepared for publication three other studies on the projections of the vLGN using the autoradiographic technique have been published. In one of them, Edwards, Rosenquist and Palmer⁹ described the projections of this nucleus in the cat, and in the other two, Graybiel¹¹ and Swanson, Cowan and Jones³⁷ considered the projections from the vLGN of the rat and the cat. At this point it may be stated that, in the present study on the rat, basically the same projections described by Swanson, Cowan and Jones³⁷ were found, but in addition another site of termination of the vLGN neurons was encountered in the pons as described by Edwards, Rosenquist and Palmer⁹ and Graybiel¹¹. In the present article, a different interpretation of the mode of termination of projections to some structures is given and there is a different interpretation of the pathways taken by some of the vLGN axons to reach these structures. Because of these differences, it was deemed appropriate to present our results.

MATERIALS AND METHODS

Injections

All of the radioisotope injected was drawn from a concentrated solution of L-[2,3-³H]proline (New England Nuclear, specific activity 37.3 Ci/mmol). This solution was prepared by evaporating off the 5 ml of solvent in which the proline was delivered and redissolving the residue in 250 μ l of saline. Thus a 20 times concentrated solution was prepared.

The injection system was a hydraulic one consisting of a Harvard Apparatus Peti-pump 1150 which advanced the thumb-piece of a 10 μ l Hamilton syringe that was filled with water and connected to a glass micropipette via a length of Intramedic polyethylene tubing (PE 20). The two junctions at either end of the tubing were sealed with vacuum grease. The system was made air-free to ensure that the injection of the labeled amino acid would decrease the amount of erratic pressure on the brain tissue and thereby lessen the tissue damage. After the entire system was filled with water, 2 μ l of soybean oil were drawn up into the micropipette which had a tip diameter of 20 μ m to 50 μ m. The concentrated proline solution was then drawn up behind this oil interphase.

Albino rats of 150–250 g were placed in a David Kopf stereotaxic apparatus after sedation with chloral hydrate and all injections were made stereotaxically. To make an injection the micropipette tip was passed into the ipsilateral cortex anterior to the LGN so that it made an angle of from 15° to 45° with respect to the perpendic-

ular to the surface. Total amounts of isotope injected varied from 0.4 μ l to 2.0 μ l and each injection lasted from 1 to 2 h.

Processing of tissue

Assuming fast axonal transport rates of 100–500 mm/day, survival times of 5, 24 and 30 h were used to maximize the labeling in the axon terminals of pathways emanating from the LGN. Animals which were to have their brains processed for paraffin embedding were perfused through the left ventricle of the heart with Bouin's fixative subsequent to a saline washout. Other animals intended for frozen sectioning of their brains were perfused with either a 4% paraformaldehyde solution or the two perfusion mixtures of glutaraldehyde and paraformaldehyde as suggested by Brightman and Reese⁴. Of the latter fixative, first the dilute and then the concentrated solutions of these mixtures were employed according to the schedule described by Peters³⁰ in order to gain good fixation for a later series of electron microscopic autoradiographic studies of the visual cortex.

Brains were dissected out the day after the fixation. Paraffin-embedded brains were sectioned at 10 μ m while frozen sectioning was done at 30 μ m. In animals used for electron microscopic analysis, the visual cortex was taken out separately, post-fixed in osmic acid and then embedded in Araldite.

Autoradiography

All sections were dipped according to the method of Kopriwa and LeBlond¹⁸ using the Kodak NTB-2 emulsion. The paraffin sections were deparaffinized in xylene prior to dipping. The frozen sections were prepared for dipping following the procedure of Hendrickson, Moe and Noble¹⁵. Groups of 5 slides were dipped in the melted emulsion which was maintained at 40 °C in a water bath and afterwards the slides were dried in the air for an hour before being stored in light-tight boxes for an exposure period which was usually three weeks long. After this time had elapsed slides were developed in Dektol for 2½ min at 17 °C. They were then washed briefly in water, immersed for 5 min in rapid fix and washed for an hour in water before being stained in a 0.5% solution of toluidine blue for cytoarchitectonic evaluation.

Analysis

Following the deposition of [³H]proline into the neuropil of the LGN subsequent to an injection, label was continually acquired by and incorporated into protein within each cell, because this was not a pulse label followed by a washout. Therefore, a continual flow of labeled proteins down the axon occurred via the fast axonal transport and there was not a flow of one distinct band of radioactivity. Thus, when examining autoradiographs, any individual silver grain at a distance from the injection site could represent radioactivity either in an axon or an axon terminal. However, in utilizing short survival times for the maximization of the fast axonal transport, it has been shown that axon terminals are labeled in preference to the axon itself^{7,17}. The methods chosen for the analysis of autoradiographs have attempted to take these considerations into account.

In area 17 of the cerebral cortex, grains were counted by using a 100 \times oil

immersion lens and a grid reticule in the eyepiece. This reticule was a square composed of 100 equal-sized boxes arranged in 10 rows. During the counting of grains through the depth of the cortex, the top bar of the first row of boxes was aligned over the pial surface. The two top rows of boxes (*i.e.*, 20 boxes) outlined a 1125 sq. μm area of labeled cortex and the silver grains within this area were counted. The next and deeper area of cortex to be counted was outlined by the middle two rows of the reticule, so that the intervening two rows of boxes were omitted. This alternating pattern of counting two rows and skipping the next two rows was continued until the white matter was reached. The background count was obtained by averaging the number of grains present over a similar sized area in an adjacent part of the cerebral cortex which did not show a definite labeling pattern. Similar grain counts were made over the superior colliculus.

For three animals graphical representation of the distribution of silver grains in area 17 was generated from raw data obtained in the manner described above. Assuming the peak count in layer IV to be 100%, all other counts in the same traverse were calculated as a percentage of this maximum grain count. A number of traverses were carried out in different parts of area 17 in each animal and the data from each traverse were plotted separately.

To determine the paths of axons projecting from the neurons of the vLGN, and to assess the sites of termination of these axons, structures were assumed to be labeled when the number of grains covering them was significantly above that of the neighboring structures. When fiber tracts contained label it was found that the silver grains overlying them were arranged in, and confined to, distinct bands. This appearance was so characteristic that labeled fiber bundles could even be distinguished in the areas of high background grain counts close to the site of injection.

To more definitely identify the brain stem structures showing labeling, the sites of high activity in the autoradiographic sections were studied secondarily in sections of control brains stained by Klüver–Barrera and silver techniques.

RESULTS

In this study, 7 rats exhibited labeled injection sites in the LGN complex. Another 14 rats had labeling in other parts of the thalamus or in the overlying hippocampus. Three different injections into the LGN are illustrated in Fig. 1 which also shows a Klüver–Barrera stained section through approximately the same level of the brain stem. Rats numbered 98 and 100 (Fig. 1D) had injections confined to the vLGN. Rats 66 (Fig. 1C) and 69 had injections which included portions of both the dorsal vLGN and the ventral dLGN. The injection site of rat 102 included the lateral aspect of each of the subdivisions of the LGN while in rat 56 (Fig. 1B) the injection site included the entire dLGN and a dorsal portion of the vLGN. Rat 101 had a large injection that labeled the entire LGN complex as well as the medial geniculate nucleus, the lateral posterior nucleus and the ventrobasal complex of the thalamus. In the process of labeling the LGN, some label invariably diffused into the adjacent parts of the hippocampal formation and dentate gyrus, but the projections from these latter areas are not discussed here.

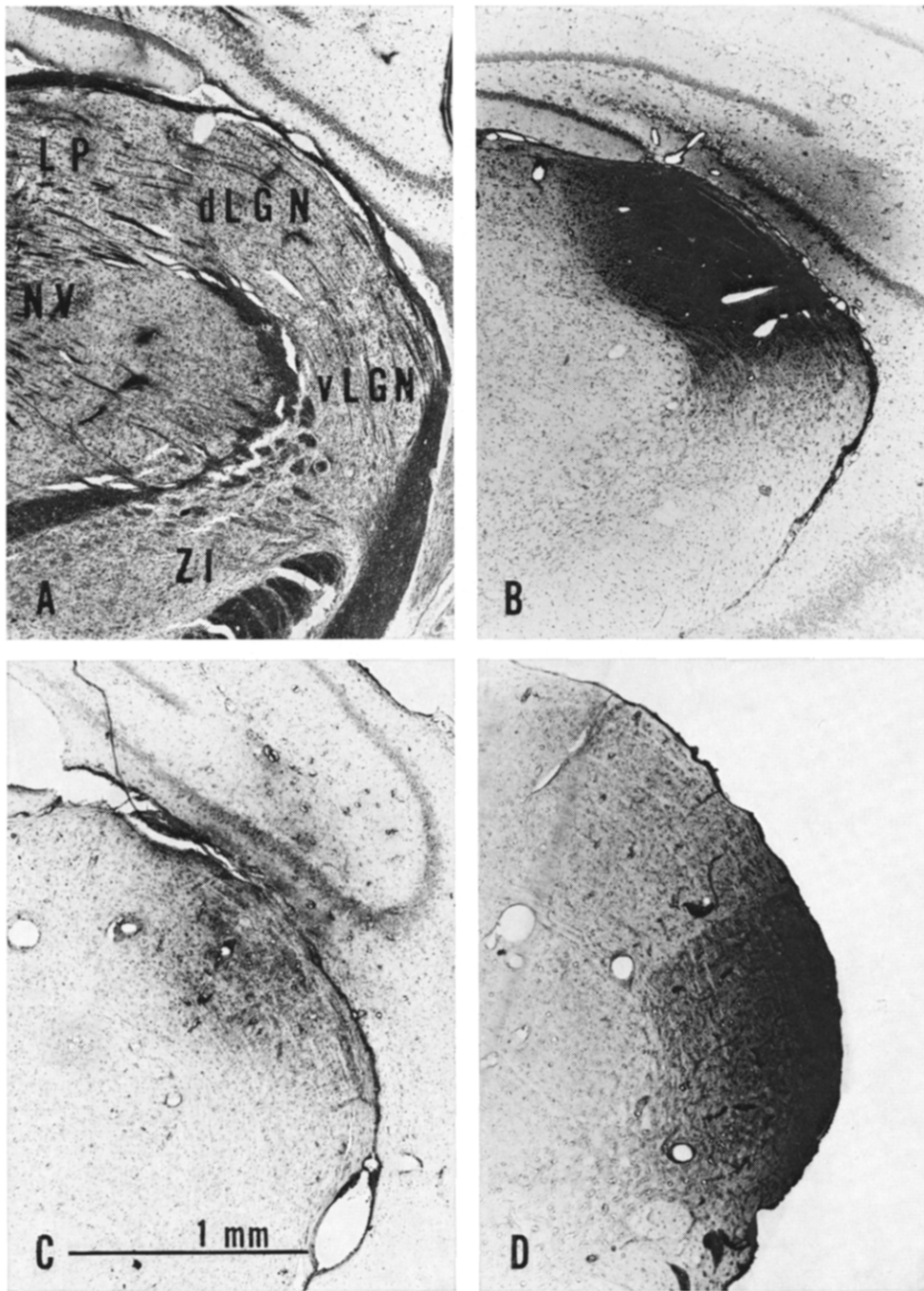


Fig. 1 Low power photomicrographs of coronal sections through the lateral geniculate body of the rat brain stem. Fig. 1A is a Kluver-Barrera-stained preparation showing the relationship of neighboring structures to the lateral geniculate body (dLGN and vLGN). These structures are the zona incerta, ZI, the ventral nucleus of the thalamus, NV, and the lateral posterior nucleus, LP. Fig. 1B is a Nissl-stained section showing the injection site of rat 56 in an autoradiograph at about the same level as Fig. 1A. Notice that the entire dLGN is labeled as well as a small dorsal portion of the vLGN. The amount of radioisotope injected was $1.0 \mu\text{l}$. Fig. 1C, from rat 66, illustrates the site of injection which includes parts of the dLGN and vLGN. The injected amount in this case was $0.4 \mu\text{l}$. Fig. 1D is a lightly stained frozen section showing the heavy labeling of the vLGN of rat 100. The center of the injection is located laterally to the vLGN in this experiment where $2.0 \mu\text{l}$ of $[^3\text{H}]$ proline was injected. Shrinkage for this brain was less than for brains of rats 56 and 66 because they were processed for paraffin embedding. The calibration line can be applied to all photomicrographs in this figure. For explanation of abbreviations used in this and following figures see pp. 366-367.

Another aspect of these injections was the effect produced as the glass micro-pipette passed through brain structures to reach the LGN. The injections made at 45° to the pial surface usually leaked labeled amino acid into the cerebrospinal fluid-filled space anterior to the LGN. This caused some labeling of ependymal cells lining the ventricular system.

dLGN projections

Although no injections were strictly confined to the neurons in this subdivision, rat 56 will be used to illustrate the projection from this dorsal part of the nucleus to the visual cortex via the optic radiation. A series of drawings from selected autoradiographs from this experimental animal is depicted in Fig. 2. The injection site diagrammed in Fig. 2E is shown in the low power photomicrograph of Fig. 1B. Labeling due to axonal transport was not found in the visual cortex of animals such as 98 and 100, in which injections were limited to the vLGN.

Following labeling of the dLGN, the course of the broad projection of the optic radiation appeared to leave the dLGN rostromedially and to course ventral to the stria terminalis in front of the hippocampal flexure (Fig. 2F and G). Labeled axons in the caudal limb of the internal capsule coursed through the caudate nucleus as far anterior as the level of the optic chiasm and from here the labeled axons were located in the white matter underlying neocortex either anterior or lateral to the visual cortex, the site of their termination.

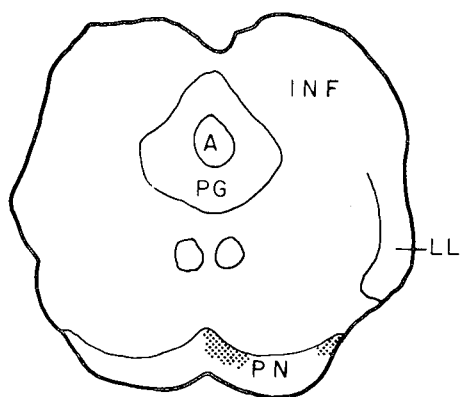
Counterstained autoradiographs of the visual cortex were examined to assess which areas of the cortex received the geniculocortical projection. Krieg¹⁹ parceled the occipital region of the cortex of the albino rat into visual areas 17, 18 and 18a. In differentiating between these areas, it may be briefly stated that in Nissl preparations area 17 was characterized by having a prominent layer IV consisting of small and densely packed granule cells. The thickness of layer IV was equal to that of the combined thickness of layers II and III. Layer V of area 17 was characterized by the presence of medium- and large-sized pyramidal cells that were scattered somewhat randomly in this thin and, compared to layers III and IV, sparsely cellular layer.

A quite sharp border could be discerned between area 17 and area 18, which lies medial to 17. Compared to area 17, layer I in area 18 was thicker while layer IV was severely reduced in thickness, and layer V seemed to contain more densely packed cells.

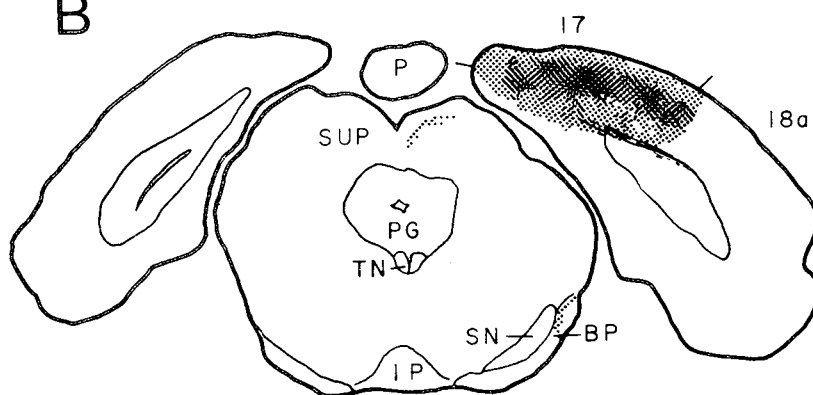
Krieg described the more laterally and caudally placed area 18a as having a less well defined border with area 17. In area 18a, he described a decrease in the concentration of granule cells in layer IV. Meanwhile, layer V was more granular than its counterpart in area 17. In the caudal part of Krieg's area 18a, where it occupies the medial border of area 17, it appeared from our observations that cytoarchitecturally this portion of the cortex was quite similar to area 17. Here, layer IV remained thick and packed with granule cells, but, because of the curvature of the cerebral hemisphere, layers II and III were relatively thinner, so that layer IV moved closer to the surface of the cortex.

In the autoradiographs of the visual cortex from rat 56, the label was heavily

A



B



C

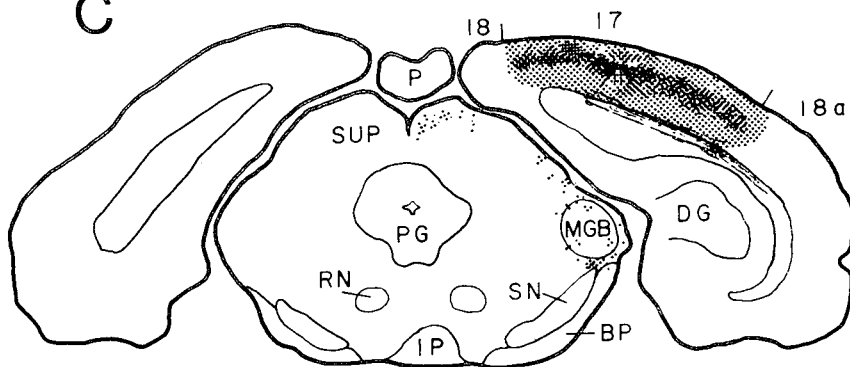


Fig 2.

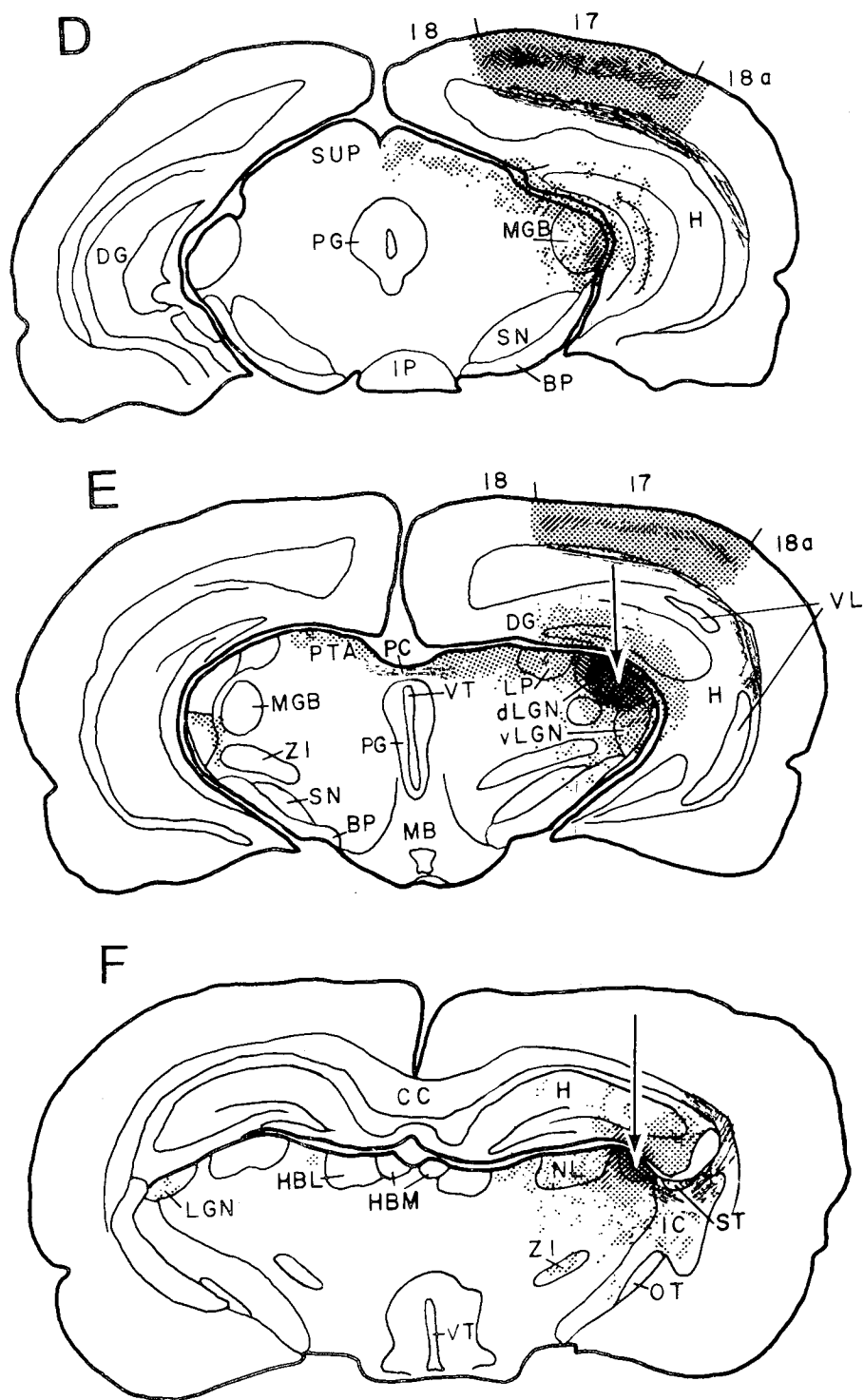


Fig. 2.

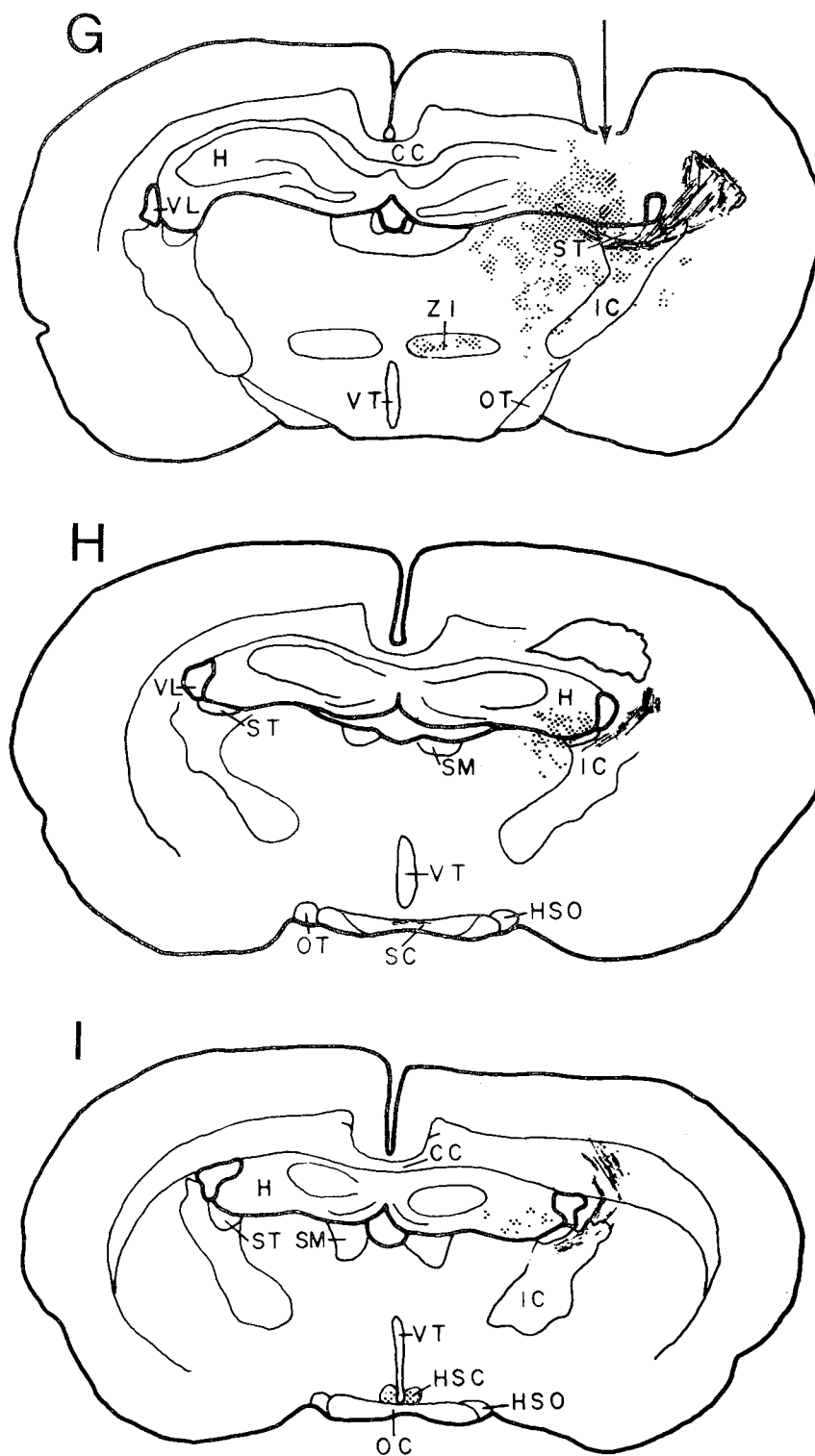


Fig. 2.

concentrated in layer IV of cytoarchitectural area 17. In this layer, the labeling was rather homogeneous and there was no tendency for it to form any type of pattern. However, there was some extension of label toward the adjacent and cytoarchitecturally defined areas 18 and 18a. This extension was slight (Fig. 2C, D and E), but indicated that the geniculocortical terminals extend into the zone of transition between areas 17, 18 and 18a.

On the medial side of the cerebral hemisphere near the caudal part of area 17 (Fig. 2B), there was an extension of the geniculocortical terminals in a portion of the cortex that Krieg²⁰ defined cytoarchitecturally as part of area 18a. However, as discussed above on the basis of our observations of Nissl-stained sections, this portion of the cortex should be included in area 17. In autoradiographs it displayed heavy labeling of layer IV and consequently it seems that both on the basis of its connections and its morphological features, this portion of the cerebral cortex is part of the primary visual cortex.

The cortical map generated from these geniculocortical projections correlated well with the primary visual area as determined by microelectrode mapping of the retinotopic organization of the visual cortex in the albino rat²⁶. The cytoarchitectonic map of striate cortex of the mouse as defined by Rose³³ also showed a caudal portion which extended into the medial side of the cerebral hemisphere. Krieg²⁰ even observed a gradual modification of the cytoarchitecture at the occipital pole where a possible interruption occurred in the ring that areas 18 and 18a form around area 17, even though he did not indicate the modification in his summary drawing.

The distribution of silver grains within the various layers of area 17 is illustrated graphically in Fig. 3 which shows the relative grain counts made on sections from three different animals. The number of traverses used to obtain the averages for each graph for animals 56, 66 and 69 were 15, 8 and 5 respectively. To combine these data the depth of the cortex from the pial surface to the junction between layer VI and the white matter was arbitrarily divided into 40 equally spaced intervals. At each of these intervals the grain counts expressed as a percentage of the layer IV maximum were read off from the individual graph and the data for separate traverses of the cortex of each animal were combined into this single representation.

A major peak of labeling appeared in layer IV in all of the animals cited in Fig. 3. This peak of labeling extended over the deeper part of layer III suggesting the presence of geniculocortical terminals in this layer. Other minor peaks coincided with the outer part of layer I and with the upper half and lowest part of layer VI.

Fig. 2. A series of tracings from autoradiographs from the brain of rat 56 from levels that were labeled caudally (A) to those that were labeled rostrally (I). The pathway of the micropipette is illustrated by the arrows in Figs. 1E, F and G. The boundaries of area 17 in Figs. 1B, C, D and E are based upon the cytoarchitectural characteristics that are discussed in the text of the paper. The stippling represents relative densities of silver grains in the autoradiographs. The broken lines represent the labeling found within the optic radiation. Although some of the sites of termination from the projections of the vLGN were labeled in this experiment, the fiber pathways were not labeled clearly so these data are represented in Fig. 5 for another experimental animal. The abbreviations used are given in the accompanying list on pp. 366-367.

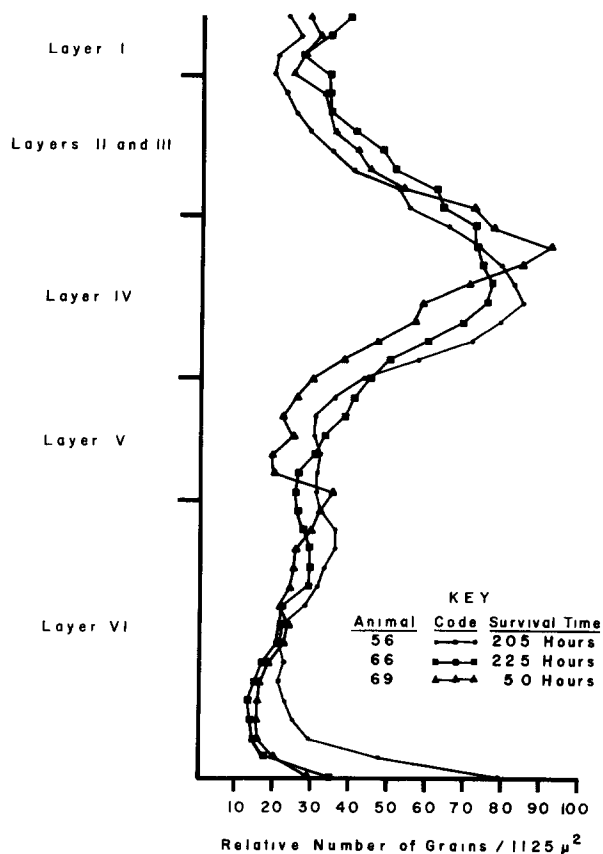


Fig. 3. A graph of the relative distribution of silver grains per unit area through the depth of area 17 of the cerebral cortex in the rat. See text for the details on the preparation of this graph. A major density peak occurs in layer IV with other minor peaks in upper layer I and in the upper half and lowest part of layer VI.

While the peak in layer I suggested the presence of axon terminals, the smaller and broader peak in upper layer VI can probably be attributed to an accumulation of label in axon terminals or in the specific thalamocortical axons as they turned from a horizontal to a vertical direction in this layer. Another explanation for this broad peak may be a branching of the thalamocortical axons which would effectively increase the total cross-sectional area of the axonal branches as compared to the cross-sectional area of the unbranched segment. The label found in the lowest part of layer VI was probably due to the horizontal organization of the geniculocortical fibers before they entered into the cortical substance²³. In traverses made through lateral parts of area 17, more label was present in the lowest part of layer VI than in the more medial parts of this area. Finally, the grain counts in the contralateral visual cortex were not above the background level, so there was no indication of a contralateral cortical projection from the dLGN.

Some raw data from one traverse made through the middle of area 17 in animal 56 is as follows. The layer IV peak reading was 233 grains/1125 sq. μm , while the

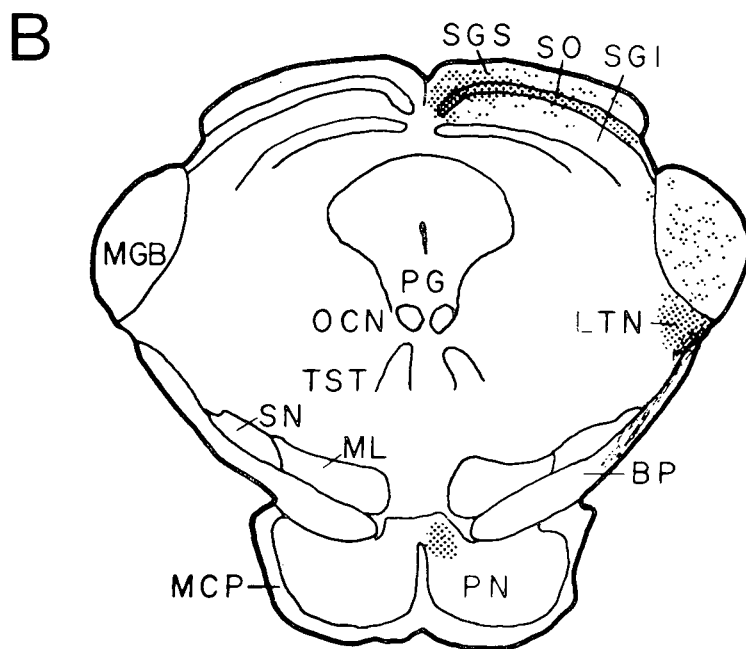
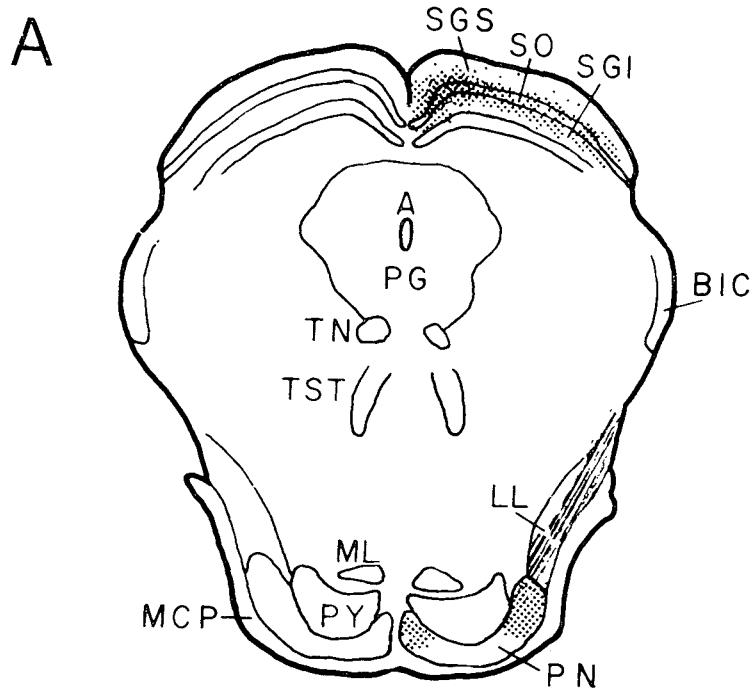


Fig. 5.

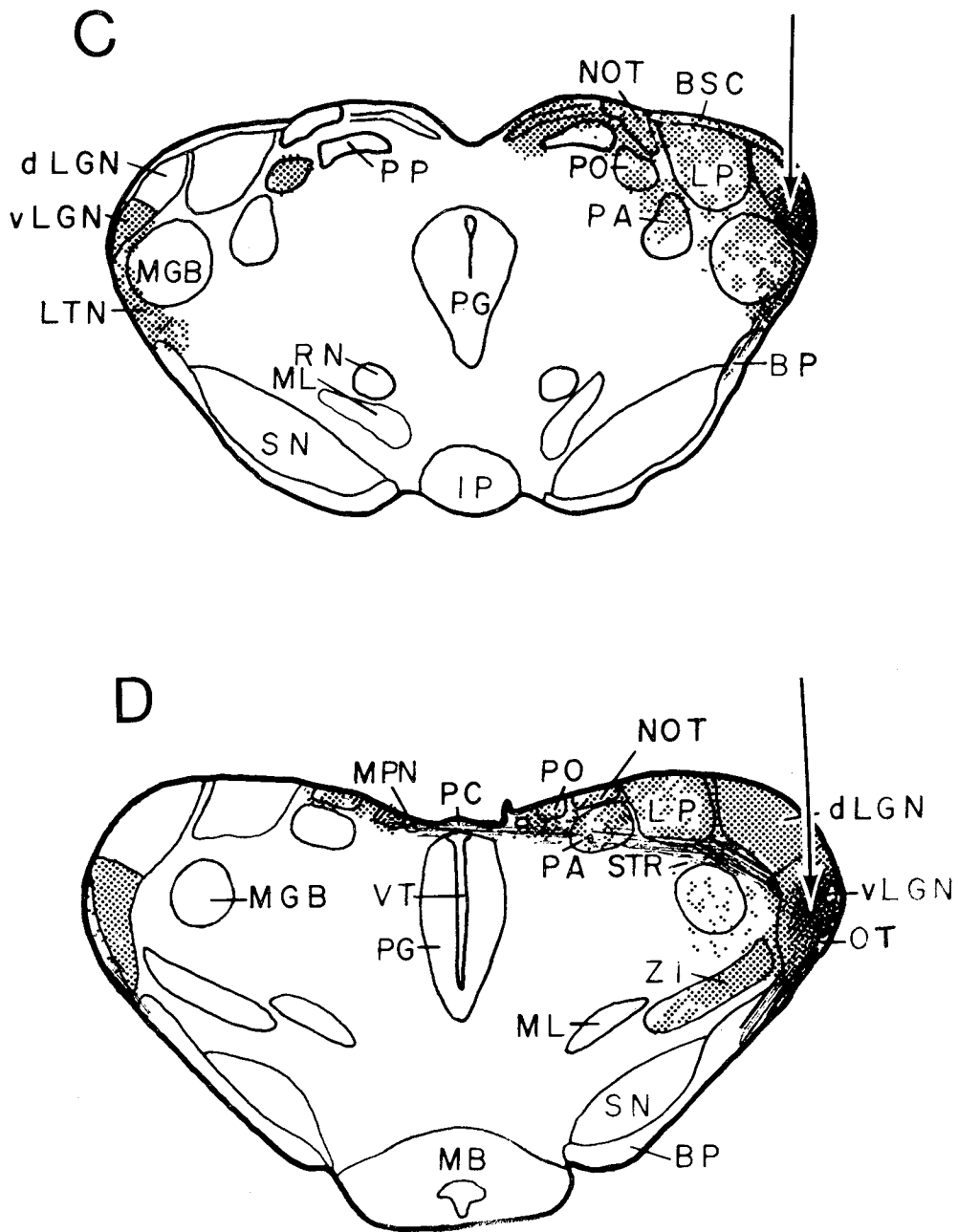


Fig. 5.

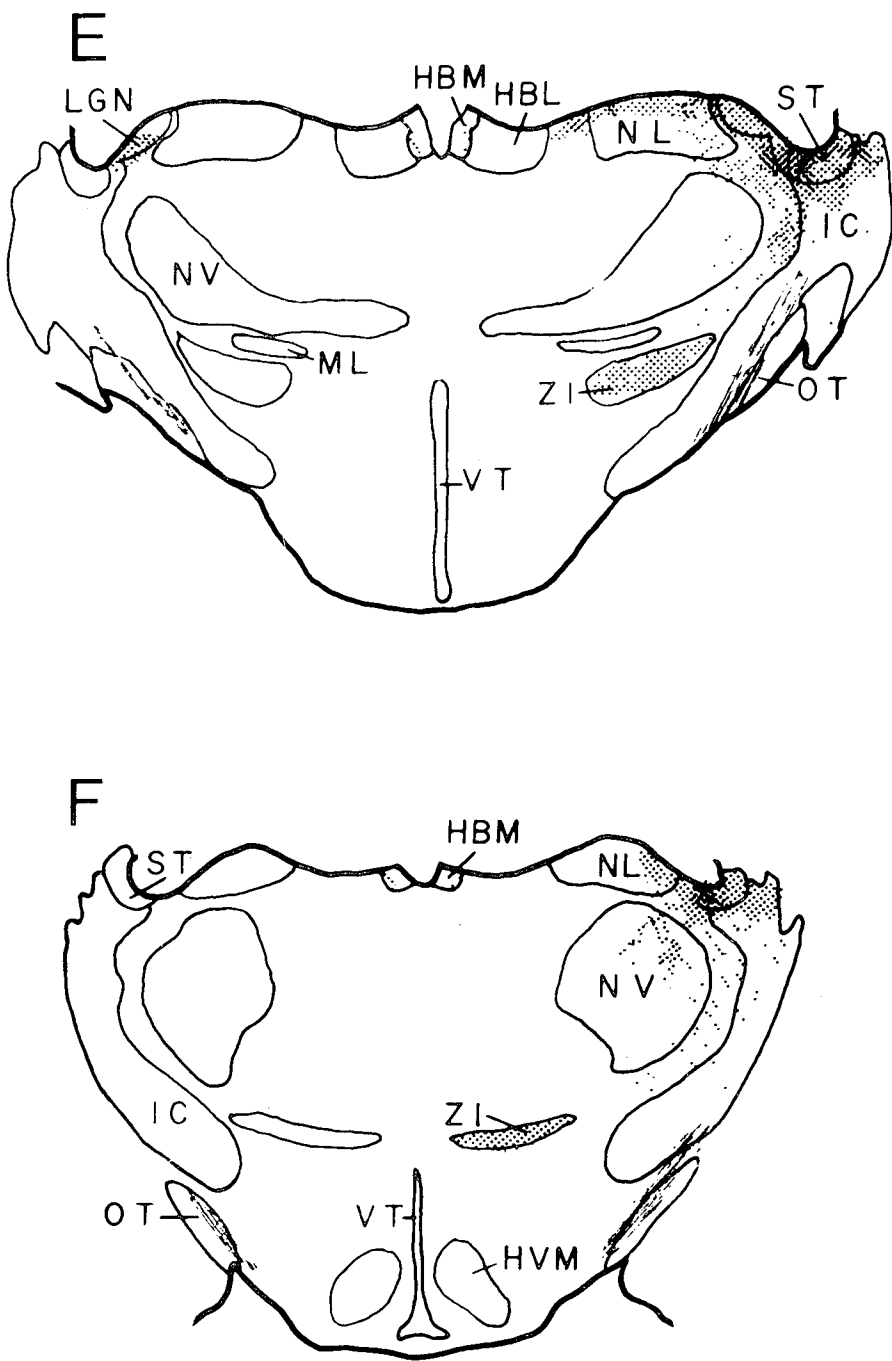


Fig. 5.

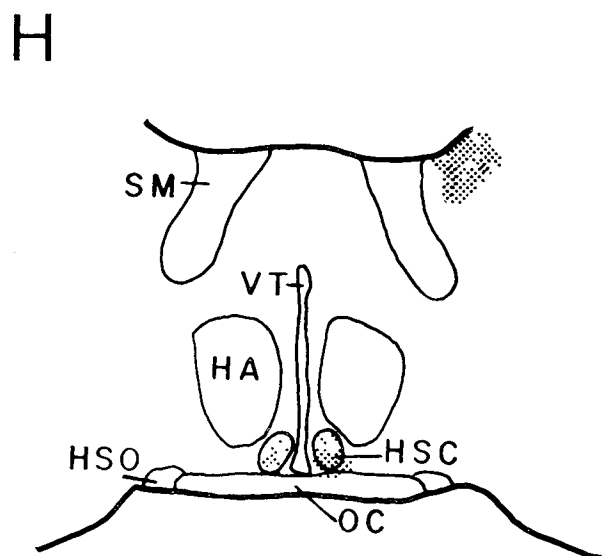
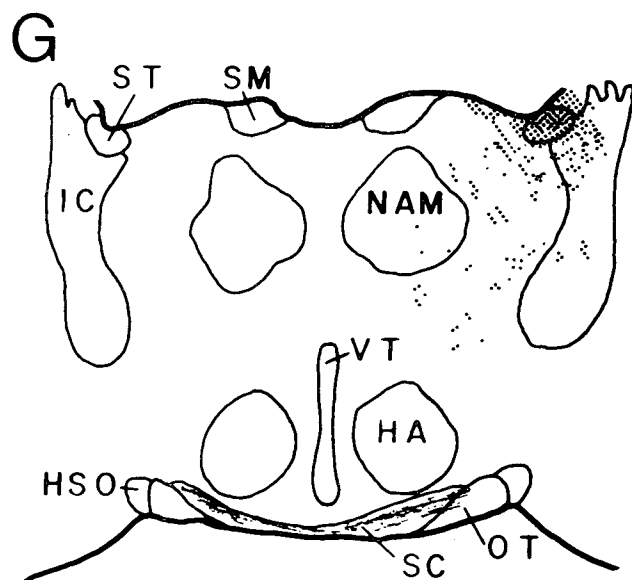


Fig. 5. A series of drawings of the brain stem of animal 100 after labeling the injection site in the ventral lateral geniculate nucleus (arrows). The stippling represents relative densities of the silver grains as seen in the autoradiographs. The broken lines are used to represent groupings of silver grains that are suggestive for labeled fiber tracts. The most caudal section depicted is 5A and the most rostral in this series is 5H.

posterior nucleus were masked by label which diffused from the nearby site of injection. After giving terminations to the ipsilateral pretectal area, labeled fibers were seen to continue into the dorsal part of the rostral posterior commissure and to extend into the contralateral pretectal area (Fig. 5D).

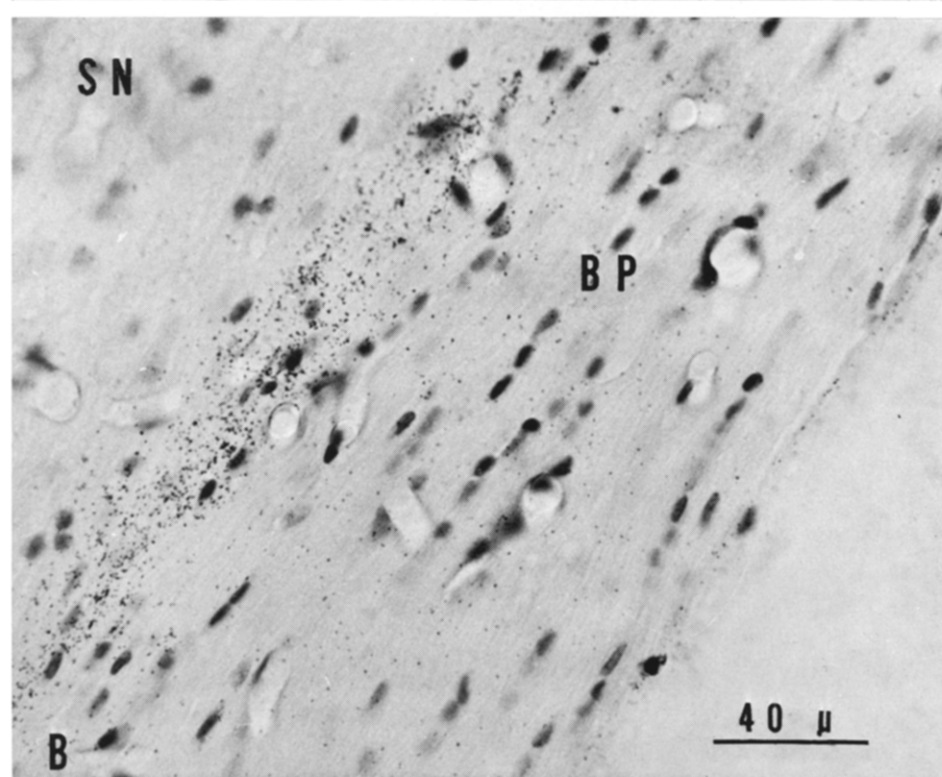
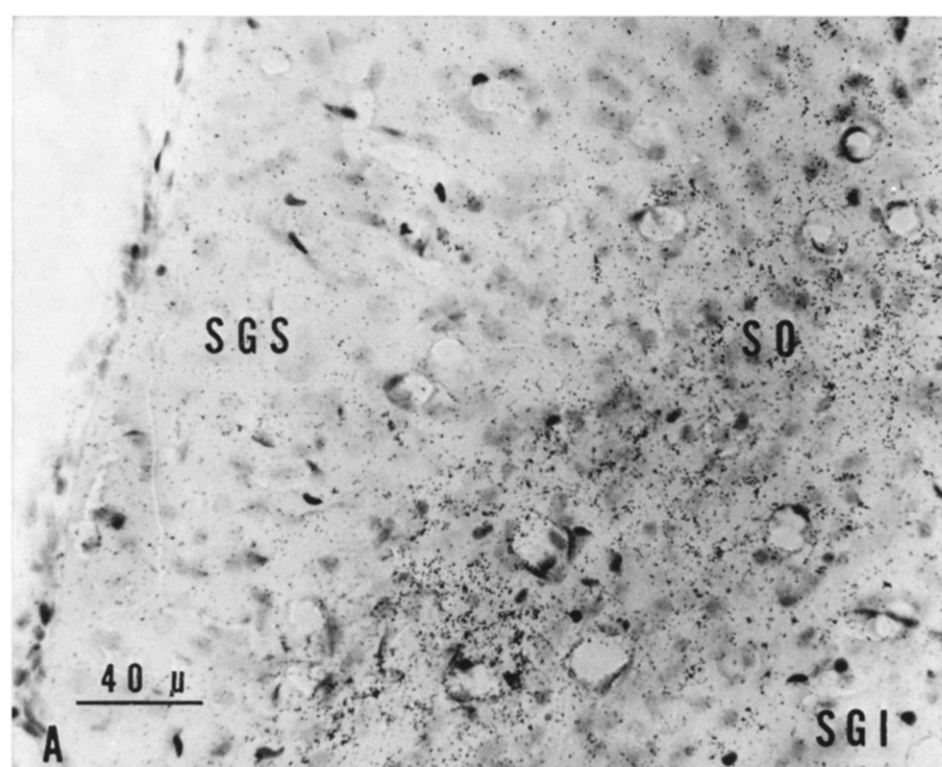
It was difficult to determine which of the specific pretectal nuclei as described by Scalia³⁶ had terminal projections from the vLGN neurons. On the side ipsilateral to the injected vLGN, it appeared that terminal labeling was primarily located in the olivary pretectal nucleus, with some additional label in the anterior pretectal nucleus and the nucleus of the optic tract. There were also some grains over the posterior pretectal nucleus, but again this could not be distinguished from labeling caused by [³H]proline which had diffused away from the injection site. Since some of the labeling of the ipsilateral medial pretectal nucleus was in the form of rows of grains, it was probably due to axons which traversed this nucleus to pass through the posterior commissure.

On the contralateral side, the labeling of terminals in the pretectal area was limited to the nucleus of the optic tract as well as to the pars oralis and pars reticularis of the olivary pretectal nucleus. On this contralateral side some label was found in the medial pretectal nucleus, but from the nature of the grain distribution it appeared that it was probably due to axons of passage. No label above background was present over the anterior and posterior pretectal nuclei.

The shortest of the ventromedial projections was to the ipsilateral zona incerta (Fig. 5D, E and F). While a projection was clearly directed towards the entire anterior extent of this subthalamic structure, it was difficult to assess if there was a projection to the part of the zona incerta adjacent to the vLGN, because of its proximity to the injection site (Fig. 5D).

A caudally directed ventromedial projection passed through the lateral terminal nucleus of the accessory optic tract (Fig. 5B) and continued in its caudal trajectory to terminate in the dorsomedial and dorsolateral parts of the pontine gray (Fig. 5A and B). This labeled geniculopontine tract passed ventrally along the medial side of the basis pedunculi (Fig. 6B) and continued along the outer face of the lateral lemniscus to enter the lateral portion of the caudal pons. A labeled tract continued across the dorsal aspect of the pyramidal tract so that it passed in a medial direction through the nucleus tegmenti pontis to terminate in the dorsomedial part of the rostral and middle pons (Fig. 7A).

Fig. 6 Terminal labeling in the superior colliculus and axonal labeling in the geniculopontine tract following injection of the ipsilateral vLGN. Fig. 6A is a high power photomicrograph from animal 100 taken from the medial part of the superior colliculus at about the level of Fig. 5A. Silver grains are found in the three layers (SGS, SO, SGI) included in the autoradiograph, however, the highest density of grains is in the stratum opticum (SO). The labeling, although present in the entire superior colliculus in these three layers (Fig. 5A, B and C), showed the highest density of silver grains in the medial third of this structure. Fig. 6B is an autoradiograph of a frozen section through the basis pedunculi (BP) ipsilateral to the injected vLGN of animal 100 showing a labeled fiber tract in its medial part adjacent to the substantia nigra (SN). The organization of the silver grains in a linear array suggests the labeling of the geniculopontine tract. The section depicted in Fig. 5B illustrates the level through the brain stem at which this photomicrograph was taken.



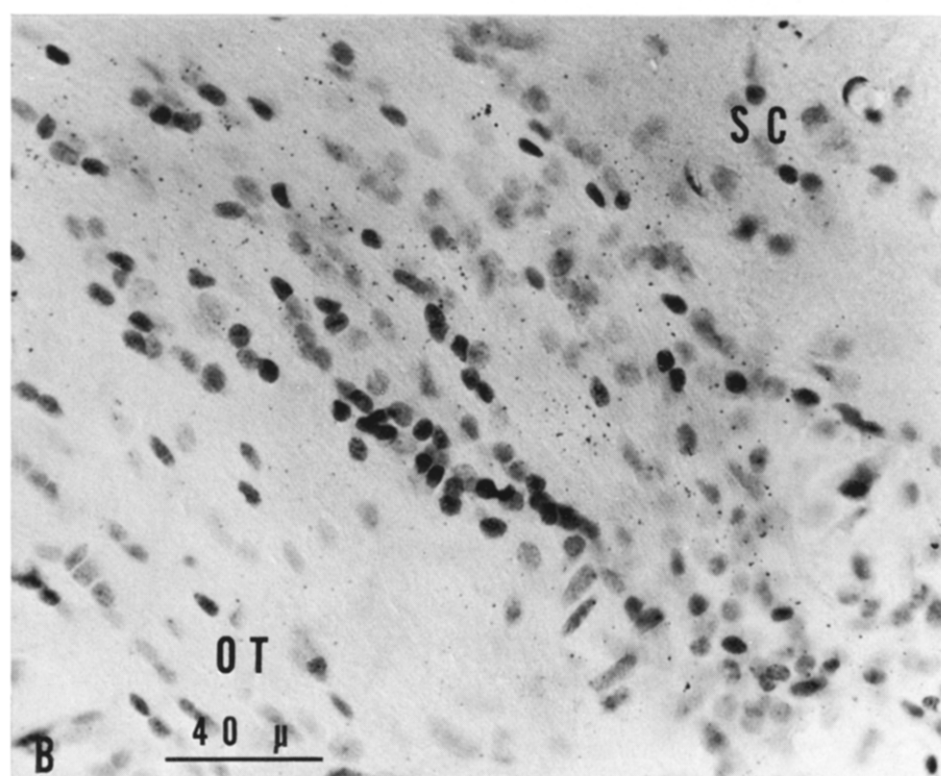
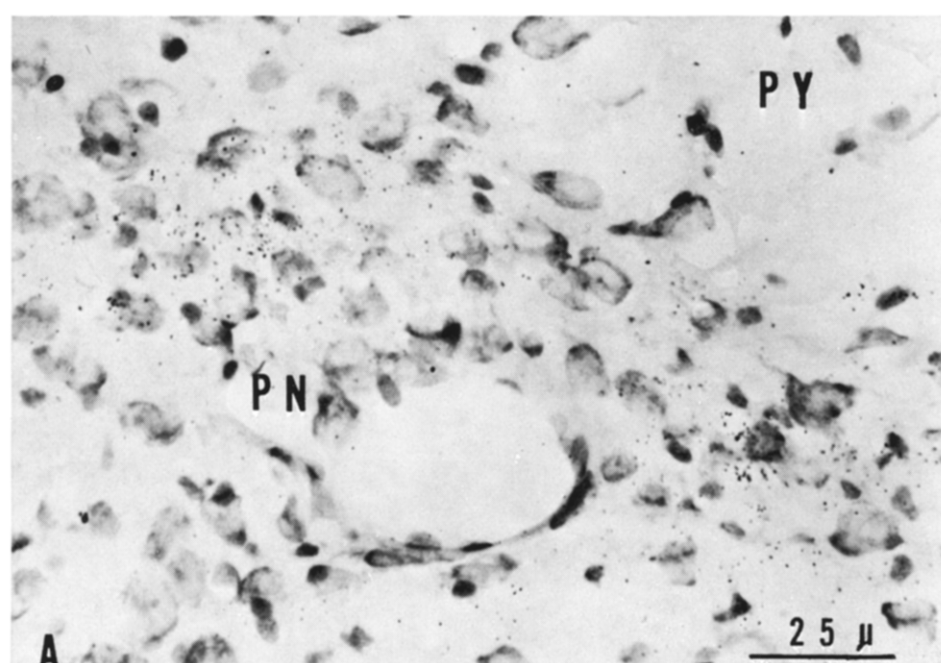
The last ventromedial projection was the longest and produced the most sites of termination along its route (Fig. 4). In coronal sections anterior to the injection site in the vLGN, there were distinct and parallel rows of silver grains coursing in the optic tract. The projection fibers were quite apparent even though the background in this area showed a high grain count because of its proximity to the vLGN. Upon approaching the optic chiasm in more anterior sections, the label was in the medial part of the optic tract (Fig. 5E and F) and about 0.5 mm caudal to the optic chiasm, there were silver grains crossing the midline (Fig. 5G). Slightly anterior to this crossing site, label appeared in the ventral regions of the suprachiasmatic nuclei on both sides of the brain stem. Although it was not quantified, it appeared that the label was about twice as dense over the ipsilateral than over the contralateral portion of this hypothalamic nucleus (Fig. 5H).

From their anterior level at the suprachiasmatic nucleus, labeled axons turned caudally in a dorsolateral direction to attain the contralateral optic tract which had silver grains arranged in rows immediately adjacent to its medial surface (Fig. 7B). The termination of this tract was in the contralateral vLGN and the lateral terminal nucleus of the accessory optic tract (Fig. 5C and D). The constant position of the labeled fibers included in this long pathway of projections corresponds to the description of the ventral supraoptic commissure or Meynert's commissure³⁹.

The extent of labeling found in the contralateral vLGN varied from one animal to another. In rats in which an entire vLGN was injected, for example rats 98 and 100, the contralateral vLGN was labeled throughout. However, in rat 56, in which only the dorsal part of the vLGN was included in the injection, the label in the contralateral vLGN was confined to the dorsal and medial portions (Fig. 2E).

As stated earlier, injections which approached the brain's surface at a 45° angle leaked more label into the cerebrospinal fluid-filled space anterior to the LGN than those made at a 15° angle off the perpendicular to the surface, with a resultant heavier labeling of the ependymal cells lining the ventricles. This former approach also caused a bilateral labeling of the medial habenular nucleus (Fig. 5E and F). Because the labeling of this latter structure was not dependent on the site of injection but was dependent on the pathway of the micropipette, it was decided that this was not a site of termination from the vLGN. However, this labeling might have been brought here from more anterior structures that project to the habenula via the stria medullaris

Fig. 7. Terminal labeling in the dorsomedial pontine gray and axonal labeling in Meynert's commissure. Fig. 7A is a high power photomicrograph of terminal labeling in the dorsomedial part of the pontine gray of animal 56 taken from a section at the same level as Fig. 2A. The labeling is heavy in two areas on either side of the blood vessel and seems to be localized over the neuropil of the pontine nucleus (PN). Notice that the dorsally located pyramidal tract (PY) is not labeled above background. Although not illustrated in this figure, there was also terminal labeling in the dorsolateral part of the pontine gray. Fig. 7B is taken from an autoradiograph of animal 100 at the level of the section depicted in Fig. 5F. The label extending diagonally across the field is present in the ventral part of the supraoptic commissure (SC), also known as Meynert's commissure, on the side contralateral to the injection site. The optic tract (OT) on the lateral aspect of the supraoptic commissure (SC) is not labeled above background levels. The labeled axons have their terminations in the vLGN and the lateral terminal nucleus on this contralateral side of the brain stem.



thalamus. The possibility exists that the medial habenular nucleus might be a structure with extreme permeability to tracers or ions in the cerebrospinal fluid similar to the area postrema³⁸.

No other labeled fiber tracts or sites of termination projecting from the vLGN were observed. No label above the background level was found in the medial terminal nucleus of the optic tract on either side or in the area between the vLGN and the pretectal area on the contralateral side. In the ipsilateral dLGN and lateral posterior nucleus the label was well above the background but neither fiber tracts nor terminals were discerned because of the masking produced by label that had diffused away from the site of injection.

DISCUSSION

In assessing the results obtained following injections into the dorsal and ventral lateral geniculate nuclei, it is essential to understand that the labeling of a structure does not necessarily indicate the presence of axon terminals. Even when short survival times are used, it is apparent from our preparations that axons are also heavily labeled. It is important to consider the distance between a labeled structure and the injection site because the radioactive amino acid can diffuse great distances, depending on the rate of delivery and the amount of isotope injected. Part of this diffusion problem can be overcome by varying the pathway of the micropipette towards the injection site. Also, the morphology of a labeled area should be studied before deciding upon the significance of the label. Thus, it is essential to study Klüver-Barrera-stained slides to observe the existence of fiber tracts that are not readily apparent in Nissl-stained autoradiographs. Another procedure which aids in the analysis of autoradiographic results is the use of multiple traverses in counting silver grains in a labeled, stratified structure. By giving adequate considerations to these points, the autoradiographic tracing method can be used successfully in tracing projections from structures deep in the central nervous system.

Following injections into the dLGN, the resultant labeling in area 17 of the rat reconfirmed the results of Lashley²² that the area striata in the rat receives a direct input from the dLGN. However, as stated earlier, the reception area for the geniculocortical fibers extends onto the medial surface of the caudal part of the cerebral hemisphere beyond Krieg's²⁰ area 17 into an area that he defined as area 18a. This area has cytoarchitectural characteristics similar to the rest of area 17, namely a thick layer IV densely packed with granule cells. It was this latter feature that allowed Rose³³ to describe a medial boundary for the caudal part of the striate area in the mouse that closely approximates the border found in this study on the rat.

Montero, Rojas and Torrealba²⁷ determined the size and location of the primary visual cortex in the rat by using microelectrode recording. In position and extent, the primary visual cortex which they defined corresponds to the part of the occipital cortex that we found to receive geniculocortical afferents. In the portion of the cortex slightly medial to the caudal boundary of Krieg's area 17, they defined receptive

fields from the superior temporal visual quadrant of the eye. They placed lesions at the physiological boundaries of this primary visual cortex and noticed that in histological preparations these boundaries coincided with the limits of the densely packed granular cell layer, layer IV. In this same study, a number of secondary visual areas were mapped in the lateral and anteromedial peristriate cortices which correspond to areas 18a and 18 respectively.

The restriction of geniculocortical afferents to area 17, as defined here for the rat, has a parallel in studies of other mammals such as the opossum², the tree shrew⁸, and the monkey⁴¹. In contrast, the cat has been shown to have projections from its dLGN to both areas 17 and 18³⁴, the primary and secondary visual cortices.

The course described for the geniculocortical tract or the optic radiation seems to be similar to that in other mammalian species. It is interesting that the course seems to coincide with that taken by the projection fibers from the striate cortex back to the dLGN as reported in the rat^{10,22,29}.

From the quantitative counts of the distribution of silver grains in the primary visual area, it is clear that as in other mammalian species the bulk of the thalamic input is to layer IV^{1,24,31,34,35}. The existence of a smaller peak of labeling in layer I correlates well with findings in other mammals of the presence of some degenerating terminals in this layer after lesions have been made in the dLGN. The small density peak in the upper half of layer VI presents more of a problem in interpretation. This small peak may represent a locus of axon terminals, but is most probably due to an accumulation of label in the geniculocortical axons as they either change their direction or branch. The existence of a peak of radioactivity in layer VI of areas 17 and 18 of the cat following dLGN injections with [³H]proline has been shown by Rosenquist, Edwards and Palmer³⁴. In their preparations the density of grains is roughly 30% that of layer IV and is interpreted as a site of termination of geniculocortical afferents since it is present with both long and short survival times. Because of the possibility of layer VI endings, electron microscopic autoradiographic experiments are being conducted to obtain answers to this and other questions pertaining to the distribution and mode of termination of the geniculocortical tract.

As these results were being prepared for publication, three papers concerned with the projections of the vLGN as visualized in autoradiographic preparations have appeared in the literature. Swanson, Cowan and Jones³⁷ and Graybiel¹¹ examined the projections of the vLGN of both the rat and the cat, while Edwards, Rosenquist and Palmer⁹ examined the cat. The results of two of these studies as well as those presented here are summarized in Table I.

With the exception that they found no projection to the pons in their study of the rat, Swanson, Cowan and Jones³⁷ found terminations identical to those encountered in this study. Such a projection has, however, been reported for the rat more recently by Graybiel¹¹. There are also differences in both the layer of termination and the extent of labeling in the superior colliculus; in the extent of the projection to the contralateral vLGN; and in the axonal pathway of the projection to the supra-chiasmatic nuclei of the hypothalamus, to the contralateral vLGN and to the lateral terminal nucleus of the accessory optic tract.

TABLE I

vLGN PROJECTIONS

<i>Terminal sites</i>	<i>Rat</i>		<i>Cat</i>	
	<i>Present study</i>	<i>Swanson et al.³¹</i>	<i>Swanson et al.³¹</i>	<i>Edwards et al.⁶</i>
Pretectal area				
Ipsilateral				
Anterior n.	present	present	present	present
Medial n.	not present	not present	present	not reported
Nucleus of the optic tract	present	present	present	not reported
Olivary n.	present	present	not reported	present
Contralateral				
Anterior n.	not present	not present	not present	not present
Medial n.	not present	not present	present	not reported
Nucleus of the optic tract	present	present	present	present
Olivary n.	present	present	not present	not present
Superior colliculus	entire extent	rostral third		
Stratum griseum superficiale	present	present	present	present
Stratum opticum	medial third	present	present	present
Stratum griseum intermediale	present	lateral half	present	present
Zona incerta				
Ipsilateral	present	present	present	present
Contralateral	not present	not present	present	not reported
Pons	dorsal portions of medial and lateral parts	not reported	not reported	rostradorsal part of paramedial gray
Lateral terminal n. of the accessory optic tract				
Ipsilateral	present	present	present	not reported
Contralateral	present	present	present	not reported
Medial terminal n. of the accessory optic tract	not present	not present	not reported	present
Contralateral vLGN	entire vLGN	limited to dorsal portion	present	not reported
Suprachiasmatic n.				
Ipsilateral	present	present	present	not reported
Contralateral	present	present	present	not reported

In the present study an injection of the vLGN resulted in a heavy projection to the stratum opticum of the superior colliculus, especially to its medial one-third. In rat 56, where the injection site was similar in size and location to rat R49 in the article by Swanson, Cowan and Jones³⁷, the projection was not so apparent, but on the basis of our grain counts there was a distinct density peak in the stratum opticum. In contrast, Swanson, Cowan and Jones³⁷ found a heavily labeled projection to the lateral part of the stratum griseum intermediale. They also reported silver grains only

in the rostral one-third to one-half of the superior colliculus, whereas our observations have demonstrated labeling throughout the entire rostrocaudal extent of this structure.

A second difference between this work and that of Swanson, Cowan and Jones³⁷ involves the vLGN projection to the contralateral vLGN. When the vLGN was entirely injected in our material, there was a complete labeling of the contralateral vLGN. If only the dorsal part of the vLGN was labeled as in rat 56 of this report, and R49 of Swanson, Cowan and Jones³⁷, there was label only in the dorsal and medial parts of the contralateral vLGN. Taken together these results seem to indicate an organized commissural projection, although small and more localized injections must be employed to conclusively demonstrate this point.

In our rat 100 Meynert's commissure was labeled, as it was in three other animals with large injections of the vLGN. However, Meynert's commissure did not show any appreciable labeling in two cases in which only the dorsal part of the vLGN was included in the injection site. This evidence taken in conjunction with the results of the unique study of Tsang³⁹ give adequate support for this long ventromedial commissural connection for the vLGN. In order to study the pathway of the axons in the supraoptic and postoptic commissures alongside the optic tract and at the optic chiasm, Tsang blinded young rats so that the optic tract would degenerate and give a less complicated picture of these specific areas in Golgi-Cox stained material. From his observations, he suggested the following. 'The commissural bundle diminishes in size after its entrance into the LGB. This suggests that some of its fibers terminate (or originate) in this structure, especially its ventral nucleus'. The existence of this commissural pathway in the rat must give some hint of a similar one in other mammals especially the cat where it is now known that a projection exists to the contralateral vLGN^{11,37}.

Comparatively, the three studies of the vLGN projections, as summarized in Table I, as well as that of Graybiel¹¹, demonstrate that the projections of this nucleus are similar in the rat and the cat. Both have ipsilateral projections to the superior colliculus, the zona incerta and the pons; bilateral projections to the pretectal area, lateral terminal nuclei of the accessory optic tract and the suprachiasmatic nuclei of the hypothalamus; and a contralateral projection to the vLGN. In the cat, there is a slight difference in the projection to the pons, for only a medial projection was observed. A major difference between these two mammals is that the cat vLGN has two projections that are lacking in the rat. These are projections to the ipsilateral medial terminal nucleus of the accessory optic tract and to the contralateral zona incerta. In this study no projection to the ipsilateral or contralateral medial terminal nucleus was observed. This nucleus, however, is a site of termination for retinal ganglion cells¹⁴. A contralateral projection to the zona incerta was only observed in rat 101. However, the injection site in this experiment included the ipsilateral zona incerta and therefore the results of this injection cannot be construed to indicate a projection from the vLGN.

In conclusion, the vast range of projections from the vLGN shows that this nucleus is important in many subcortical visual functions. The fact that the vLGN projects to many of the same sites as the retina and visual cortex underscores its

importance in the processing of visual stimuli encoded in the nervous system. In the rat, both the retina^{13,14,16,28,36} and the vLGN have overlapping bilateral inputs to the suprachiasmatic nuclei, the lateral terminal nuclei and certain pretectal nuclei and contralateral inputs to the vLGN. The visual cortex²⁹ and the vLGN share ipsilateral projections to certain pretectal nuclei, the zona incerta and the lateral dorsum of the pons. It is known that the three most superficial layers of the superior colliculus receive afferents from the retina and the visual cortex. Now, a third, and suspected²⁵, source of visual information has been demonstrated to come from the vLGN. Also, the visual cortex projects mainly to the lateral two-thirds of the superior colliculus which complements the projection of the vLGN to the medial one-third.

It has become apparent from these results, as well as the work of Graybiel¹¹, that there is a vast amount of interaction in the various brain stem nuclei associated with the visual pathways. There is a strong possibility that these converging projections allow spatial and temporal summation in some of these terminal structures. Recent physiological recordings from single units of the vLGN of the cat and the pregeniculate nucleus of the monkey have shown the responsiveness of cells in these nuclei to head rotation and eye movements, respectively^{5,32}. Future physiological recordings may determine the nature of the summation in other nuclei receiving visual information.

ABBREVIATIONS

A	= cerebral aqueduct	ML	= medial lemniscus
BIC	= brachium of the inferior colliculus	MPN	= medial pretectal nucleus
BP	= basis pedunculi	NAM	= anterior medial nucleus of the thalamus
BSC	= brachium of the superior colliculus	NL	= lateral nucleus of the thalamus
CC	= corpus callosum	NOT	= nucleus of the optic tract
DG	= dentate gyrus	NV	= ventral nucleus of the thalamus
H	= hippocampus	OC	= optic chiasm
HA	= anterior nucleus of the hypothalamus	OCN	= oculomotor nucleus
HBL	= lateral habenular nucleus	OT	= optic tract
HBM	= medial habenular nucleus	P	= pineal body
HSC	= suprachiasmatic nucleus of the hypothalamus	PA	= anterior pretectal nucleus
HSO	= supraoptic nucleus of the hypothalamus	PC	= posterior commissure
HVM	= ventromedial nucleus of the hypothalamus	PG	= periventricular gray
INF	= inferior colliculus	PN	= pontine nucleus
IP	= interpeduncularis nucleus	PO	= olivary pretectal nucleus
IC	= internal capsule	PP	= posterior pretectal nucleus
LGN	= lateral geniculate nucleus	PTA	= pretectal area
dLGN	= dorsal lateral geniculate nucleus	PY	= pyramidal tract
vLGN	= ventral lateral geniculate nucleus	RN	= red nucleus
LL	= lateral lemniscus	SC	= supraoptic commissure
LP	= lateral posterior nucleus	SGI	= stratum griseum intermediale of the superior colliculus
LTN	= lateral terminal nucleus of the accessory optic tract	SGS	= stratum griseum superficiale of the superior colliculus
MB	= mammillary body complex	SM	= stria medullaris thalami
MCP	= middle cerebellar peduncle	SN	= substantia nigra
MGB	= medial geniculate body	SO	= stratum opticum of the superior colliculus
		ST	= stria terminalis

STR	= superior thalamic radiation	VL	= lateral ventricle
SUP	= superior colliculus	VT	= third ventricle
TN	= trochlear nucleus	ZI	= zona incerta
TST	= tectospinal tract		

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